CHAPTER III

ANALYSIS OF THE POPULATION MODELS

In this chapter dynamics of a general delay population model will be analysed. Firstly, we investigate the equilibria of the selected model, and then the linearisation technique about the equilibria will be applied to transform the nonlinear model to be a linear problem, called the linearised system. Moreover, the theorems in the previous chapter will be used to determine stability properties including a Hopf bifurcation of each equilibrium of the selected model.

The main aim in this chapter is to find the sufficient conditions for asumptotic stability and the existence of a Hopf bifurcation. The analytical results will be shown *via* some related problems, such as the Mackey-Glass equation and the Nicholson's blowflies equation. Finally, we use an advantage of Matlab® programming to illustrate numerical solutions of the selected problems and show their dynamical behaviours.

3.1 The General Population Model with a Delay

There are various types of population models which can be used in a real problem. In general the rate of change of the number of population depends on death-rate and birth-rate. General model of the rerated rate of population change is

$$\frac{dN}{dt} = -\Big(\text{death rate}\Big) + \Big(\text{growth rate}\Big),$$

where $N(t)$ is the population size at the present time t. Here we aim to analyse the population models with a constant delay of the form

$$N'(t) = -\gamma N(t) + \beta f(N(t-\tau))N(t-\tau). \tag{3-1}$$

Note that $N(t)$ is the total population size, $f(N)$ is a birth-rate function, $\beta > 0$ represents a birth-rate constant, $\gamma > 0$ refers to the death-rate constant, and τ is a positive delay. In population problems, the time $t - \tau$ may represent the time in the past state or time delay. Function f is the birth-rate function which depended on the number of population N. In this study the birth-function f is assumed as follows:

(H1) function f is continuous and f^{-1} can be determined,
(H2) function $f(x)$ is positive for $x \geq 0$,
(H3) function $f(x)$ is a decreasing function for $x \geq 0$.

To find the equilibria, let $\tilde{N}$ be an equilibrium of (3-1), and set $N'(t) = 0$ and $N(t) = \tilde{N}$, then (3-1) becomes

$$-\gamma\tilde{N} + \beta f(\tilde{N})\tilde{N} = 0,$$

or

$$\tilde{N}\left(-\gamma + \beta f(\tilde{N})\right) = 0. \tag{3-2}$$

From (3-2), there exists at least one equilibrium, which is the *trivial equilibrium* $\tilde{N}_0 = 0$. Moreover the assumptions (H1) and (H2) imply that there also exists another equilibrium $\tilde{N}_+ = f^{-1}(\gamma / \beta)$, which can be positive provided that the value of $f^{-1}(\gamma / \beta)$ is positive. In the next section, stability properties for all equilibria of (3-1) will be analysed.

3.2 Stability Properties of the Selected Model

We study, in this part, the (local) stability properties of the equilibria of (3-1) using the linearisation method.

Under the assumption (H1)-(H3), and suppose that $\tilde{N}$ is the equilibrium of (3-1). Let $y(t) = N(t) - \tilde{N}$, then the linearised equation of (3-1) is

$$y'(t) = -\gamma y(t) + \eta y(t - \tau), \tag{3-3}$$

where

$$\eta = \beta\big(f(\tilde{N}) + \tilde{N}f'(\tilde{N})\big). \tag{3-4}$$

Note that if $\tilde{N} = 0$, then (3-4) becomes $\eta = \beta f(0)$. We can see that (3-3) has only one equilibrium, namely the trivial equilibrium $\tilde{y} \equiv 0$. To find the characteristic equation of (3-3), let $y(t) = e^{\lambda t}$ be the solution of (3-3), where λ is the eigenvalues or roots of the characteristic equation. Replace $y(t) = e^{\lambda t}$ to (3-3), then we have

$$\lambda e^{\lambda t} = -\gamma e^{\lambda t} + \eta e^{\lambda(t-\tau)}.$$

Thus the characteristic equation of (3-3) is

$$\lambda = -\gamma + \eta e^{-\lambda\tau}. \tag{3-5}$$

In addition, to determine stability properties for each equilibrium of (3-1), we need to verify that all roots λ_i of (3-5) have negative real parts. Applying Theorem 2-6 in Chapter II, it is not difficult to show that all eigenvalues have negative real-part provided that $\gamma > |\eta|$. Moreover, when we apply Lemma 2-7 to our problem, the stability properties of the equilibria of (3-1) with linearised equation (3-3) can be stated in the following theorem.

Theorem 3-1

Suppose that $\tau > 0$ *and* $\eta = \beta\big(f(\tilde{N}) + \tilde{N}f'(\tilde{N})\big)$. *Let* $\tilde{N}$ *be an equilibrium of* (3-1). *Then the stability properties of* $\tilde{N}$ *are as follows.*

(1) If $\gamma > |\eta|$, *then* $\tilde{N}$ *is asymptotically stable.*

(2) If $\gamma < \eta$, *then* $\tilde{N}$ *is unstable.*

(3) If $\eta < 0$ *and* $-\gamma > \eta$, *then* $\tilde{N}$ *is asymptotically stable for* $\tau \in [0, \tau_0)$, *and it is unstable for* $\tau > \tau_0$.

Proof To prove Theorem 3-1, we can apply Lemma 2-7 directly to (3-1). It can be seen that $A = -\gamma$ and $B = \eta$, then the stability properties of (3-1) can be stated in Theorem 3-1. ■

In general, Theorem 3-1 provides the sufficient conditions for the equilibrium $\tilde{N}$ of (3-1) to be stable or unstable. In addition, condition (3) shows that the delay can switch stability. Let τ be the bifurcation parameter. We can see from condition (3) in Theorem 3-1 that $\tau = \tau_0$ is a bifurcation point. Hence, the conditions $\eta < 0$ *and* $-\gamma > \eta$ are sufficient conditions for the bifurcation parameter τ undergoes a bifurcation.

In the next section we will investigate additional conditions and provide the formula in which $\tau = \tau_0$ becomes the Hopf bifurcation point.

3.3 Analysis of the Hopf Bifurcation

In Chapter II, some definitions and related theorems for the occurrence of a Hopf bifurcation have been presented. In this section, we use them to determine sufficient conditions for the existence of a Hopf bifurcation. From (3-5), we restate the characteristic equation of (3-3) as follow:

$$\lambda = -\gamma + \eta e^{-\lambda\tau} \tag{3-6}$$

Suppose that $\omega \in \mathbb{R}$, and let $\lambda = \pm i\omega$ be roots of (3-6). It follows that

$$\begin{aligned} i\omega &= -\gamma + \eta e^{-i\omega\tau} \\ &= -\gamma + \eta(\cos\omega\tau - i\sin\omega\tau), \end{aligned}$$

or

$$\gamma + i\omega = \eta\cos\omega\tau - i\eta\sin\omega\tau. \tag{3-7}$$

Comparing the real and imaginary parts from both sides of (3-7), we have

$$\begin{aligned} \gamma &= \eta \cos \omega\tau, \\ \omega &= -\, \eta \sin \omega\tau. \end{aligned} \tag{3-8}$$

One can easily check that if ω is a solution of (3-8), then so is $-\omega$. Hence we focus only on the positive values of ω. It is not difficult to show that (3-8) satisfies

$$\gamma^2 + \omega^2 = \eta^2. \tag{3-9}$$

Since $\omega > 0$, (3-9) can be simplified as

$$\omega = \sqrt{\eta^2 - \gamma^2}. \tag{3-10}$$

Thus the condition for the Hopf bifurcation is that

$$|\eta| > \gamma. \tag{3-11}$$

In addition, the values of τ can be performed by (3-8), i.e.

$$\tau_k = \frac{1}{\omega} \arccos\left(\frac{\gamma}{\eta}\right) + 2k\pi, \tag{3-12}$$

where $k = 0, 1, 2, \ldots$, and ω is defined by (3-10).

Substituting ω from (3-10) into (3-12), we have

$$\tau_k = \frac{1}{\sqrt{\eta^2 - \gamma^2}} \left[\arccos\left(\frac{\gamma}{\eta}\right) + 2k\pi \right]; \qquad \eta < 0, \tag{3-13}$$

and

$$\tau_k = \frac{1}{\sqrt{\eta^2 - \gamma^2}} \left[2\pi - \arccos\left(\frac{\gamma}{\eta}\right) + 2k\pi \right]; \quad \eta > 0. \tag{3-14}$$

Conditions (3-13) and (3-14) represent the bifurcation points of (3-1). We will next investigate whether the bifurcation points τ_k are Hopf bifurcation points.

According to Theorem 2-9 in Chapter II, the parameter values $\tau = \tau_k$, where $k = 0,1,2,\ldots$ are Hopf bifurcation points of the linearised equation (3-3) provided that all $\lambda(\tau_k)$ are simple purely imaginary part, and $\mathrm{Re}(\lambda'(\tau_k)) \neq 0$. We present the main theorem from our analysis in the following theorem.

Theorem 3-2

Let $\lambda_k(\tau) = \alpha_k(\tau) + \mathrm{i}\omega_k(\tau)$ *be the roots of* (3-6) *near* $\tau = \tau_k$ *satisfying*

$$\alpha_k(\tau_k) = 0 \quad \textit{and} \quad \omega_k(\tau_k) = \omega_0,$$

where $\omega_0 \in \mathbb{R} \setminus \{0\}$ *and* τ_k, $k = 0, 1, 2, \ldots$ *are defined by* (3-13) - (3-14). *Then*

$$\mathrm{Re}(\lambda_k'(\tau_k)) = \alpha_k'(\tau_k) > 0,$$

and $\tau = \tau_k$ *are the Hopf bifurcation points of* (3-3).

Proof From (3-6), the characteristic equation is

$$\lambda = -\gamma + \eta e^{-\lambda\tau}. \tag{3-15}$$

Let λ be a function of τ, i.e. $\lambda = \lambda(\tau)$. Differentiating both sides of (3-15) with respect to τ, it follows that

$$\frac{d\lambda}{d\tau} = -\frac{\eta\lambda e^{-\lambda\tau}}{1 + \eta\tau e^{-\lambda\tau}}. \tag{3-16}$$

From (3-15), we can see that $\eta e^{-\lambda\tau} = \lambda + \gamma$.

Substituting it into (3-16), we have

$$\frac{d\lambda}{d\tau} = -\frac{\lambda(\lambda + \gamma)}{1 + \tau(\lambda + \gamma)}.$$

Suppose that $\lambda_k(\tau) = \alpha_k(\tau) + \mathrm{i}\omega_k(\tau)$, and let it has purely imaginary part $\mathrm{Re}(\lambda_k(\tau_k)) = 0$ and $\mathrm{Im}(\lambda_k(\tau_k)) = \omega_0$. then $\alpha_k(\tau_k) = 0$ and $\lambda_k(\tau_k) = \mathrm{i}\omega_0$. We can show that

$$\left.\frac{d\lambda}{d\tau}\right|_{\tau=\tau_k} = -\frac{\mathrm{i}\omega_0(\mathrm{i}\omega_0 + \gamma)}{1 + \tau(\mathrm{i}\omega_0 + \gamma)},$$

or

$$\lambda_k'(\tau) = \alpha_k'(\tau) + \mathrm{i}\omega_k'(\tau) = \frac{\omega_0^2 - \mathrm{i}\omega_0\gamma}{(1 + \tau\gamma) + \mathrm{i}\omega_0\tau}.$$

Consider only the real part, it is not difficult to see that

$$\mathrm{Re}(\lambda_k'(\tau_k)) = \alpha_k'(\tau_k) = \frac{\omega_0^2}{(1 + \tau_k\gamma)^2 + \tau_k^2\omega_0^2} > 0.$$

This completes the proof. ■

In the next section, which is the application part, we start finding the positive equilibrium which will be used to investigate η. To determine the existence of a Hopf bifurcation, the sufficient condition is $|\eta| > \gamma$. Then τ_k are Hopf bifurcation points which satisfy the following condition:

$$\tau_k = \begin{cases} \dfrac{1}{\sqrt{\eta^2 - \gamma^2}}\left[\arccos\left(\dfrac{\gamma}{\eta}\right) + 2k\pi\right]; & \eta < 0, \\[2ex] \dfrac{1}{\sqrt{\eta^2 - \gamma^2}}\left[2\pi - \arccos\left(\dfrac{\gamma}{\eta}\right) + 2k\pi\right]; & \eta > 0, \end{cases} \tag{3-17}$$

where $\eta = \beta\big(f(\tilde{N}) + \tilde{N}f'(\tilde{N})\big)$.

3.4 Applications and Numerical Examples

In this section, we will apply our results found with some birth-rate functions. To support the analytical result, we use Matlab® to show numerical behaviours including the existence of Hopf bifurcation.

From the general equation with the form:

$$N'(t) = -\gamma N(t) + \beta f(N(t-\tau))N(t-\tau). \tag{3-18}$$

Note that the in this work, we apply the our analytical results to the Mackey-Glass equation and the Nicholson's blowflies equation, which are special cases of (3-18).

3.4.1 The Mackey-Glass equation

We consider the equation which proposed by Mackey and Glass [16]

$$N'(t) = -\gamma\, N(t) + \frac{\beta\, \theta^n N(t-\tau)}{\theta^n + N^n(t-\tau)}; \qquad t \geq 0. \tag{3-19}$$

Equation (3-19) is called Mackey-Glass equation. It describes a physiological control system of the red-blood cells [10, 16]. Here, $N(t)$ represents the density of mature cells in the blood circulation, τ denotes the time delay between the production of immature cells in the bone marrow and their maturation for release in circulating bloodstreams.

To reduce parameters in the Mackey-Glass equation, let $N(t) = \theta x(t)$, and then equation (3-19) becomes

$$x'(t) = -\gamma x(t) + \frac{\beta x(t-\tau)}{1 + x^n(t-\tau)}; \qquad t \geq 0. \tag{3-20}$$

Throughout this section we assume that $\beta > \gamma > 0$ and $n, \tau \in \mathbb{R}^+$.

The equilibrium $\tilde{x}$ of (3-20) is determined by giving $x'(t) = 0$, and we need to solve $\tilde{x}$ from

$$-\gamma\tilde{x} + \frac{\beta\tilde{x}}{1+\tilde{x}^n} = 0.$$

It is not difficult to show that if $\beta > \gamma$, then there exists the unique positive equilibrium:

$$\tilde{x}_+ = \left(\frac{\beta - \gamma}{\gamma}\right)^{\frac{1}{n}}. \tag{3-21}$$

According to (3-18), we can see that

$$f(x) = \frac{1}{1+x^n}. \tag{3-22}$$

The derivative of f from (3-22) is given by

$$f'(x) = -\frac{nx^{n-1}}{(1+x^n)^2}. \tag{3-23}$$

Substitute $\tilde{x}_+$ from (3-21) into (3-22) and (3-23). Then

$$f(\tilde{x}_+) = \frac{\gamma}{\beta}, \tag{3-24}$$

and

$$f'(\tilde{x}_+) = -n\left(\frac{\gamma}{\beta}\right)^2\left(\frac{\beta-\gamma}{\gamma}\right)^{\frac{n-1}{n}}. \tag{3-25}$$

Replacing the values of $\tilde{x}_+$, $f(\tilde{x}_+)$ and $f'(\tilde{x}_+)$ from (3-21)-(3-25) to η defined in (3-4), $\eta = \beta\big(f(\tilde{x}_+) + \tilde{x}_+ f'(\tilde{x}_+)\big)$, we have

$$\eta = \gamma\left(\left(\frac{\gamma}{\beta} - 1\right)n + 1\right). \tag{3-26}$$

Finally, we can find $\tau_0, \tau_1, \tau_2, \ldots, \tau_k;\ k = 0, 1, \ldots$ from (3-13), (3-14) and (3-26):

$$\tau_k = \frac{1}{\sqrt{\eta^2 - \gamma^2}}\left[\arccos\left(\frac{\gamma}{\eta}\right) + 2k\pi\right]; \qquad \eta < 0, \tag{3-27}$$

or

$$\tau_k = \frac{1}{\sqrt{\eta^2 - \gamma^2}}\left[2\pi - \arccos\left(\frac{\gamma}{\eta}\right) + 2k\pi\right]; \quad \eta > 0. \tag{3-28}$$

As the results, the Mackey-Glass equation with the delay τ as the bifurcation parameter undergoes a Hopf bifurcation when $\tau > \tau_0$, where τ_0 is a smallest value of τ for the existence of a Hopf bifurcation.

To support the results in the previous section, we present some numerical results generated by Matlab®. The parameter values of (3-20) are placed as $n = 13,\ \beta = 5.0,\ \gamma = 0.4$, and the initial function $x(t) = 0.8$ for $t < 0$.

From (3-21), (3-24) and (3-25), it is obvious that (3-20) has unique positive equilibrium $\tilde{x}_+$ when $\beta > \gamma$. In this case we have

$$\tilde{x}_+ = 1.2067, \quad f(\tilde{x}_+) = 0.08 \quad \text{and} \quad f'(\tilde{x}_+) = -0.7929. \tag{3-29}$$

We can find η from (3-26) by replacing n, β and γ, then

$$\eta = -4.384. \tag{3-30}$$

The Hopf bifurcation point τ_0, τ_1 and τ_2 can be calculated by replacing the values of η from (3-30), $\gamma = 0.4$ and $k = 0,1,2$ into (3-27). It follows that

$$\tau_0 = 0.3807, \quad \tau_1 = 1.8199 \quad \text{and} \quad \tau_2 = 3.2592. \tag{3-31}$$

The numerical solutions of (3-19) are shown in Figure 3-1 for various values of τ. In case (a) $\tau = 0.37 < \tau_0 \approx 0.3807$, as defined in (3-31), then $\tilde{x}_+ = 1.2067$ is asymptotically stable. On the contrary, the numerical solutions which are shown in (b) $\tau = 0.39 > \tau_0$, (c) $\tau = 2.1 > \tau_1 \approx 1.8199$, (d) $\tau = 3.3 > \tau_2 \approx 3.2592$ and (e) $\tau = 6.0 > \tau_2$ are unstable, but they are oscillated about the equilibrium $\tilde{x}_+$. As the results, Hopf bifurcations can be occurred when τ is sufficiently large. Hence the positive equilibrium $\tilde{x}_+$ is asymptotically stable when $\tau \in (0, \tau_0)$, and it undergoes the Hopf bifurcations when $\tau > \tau_0$.

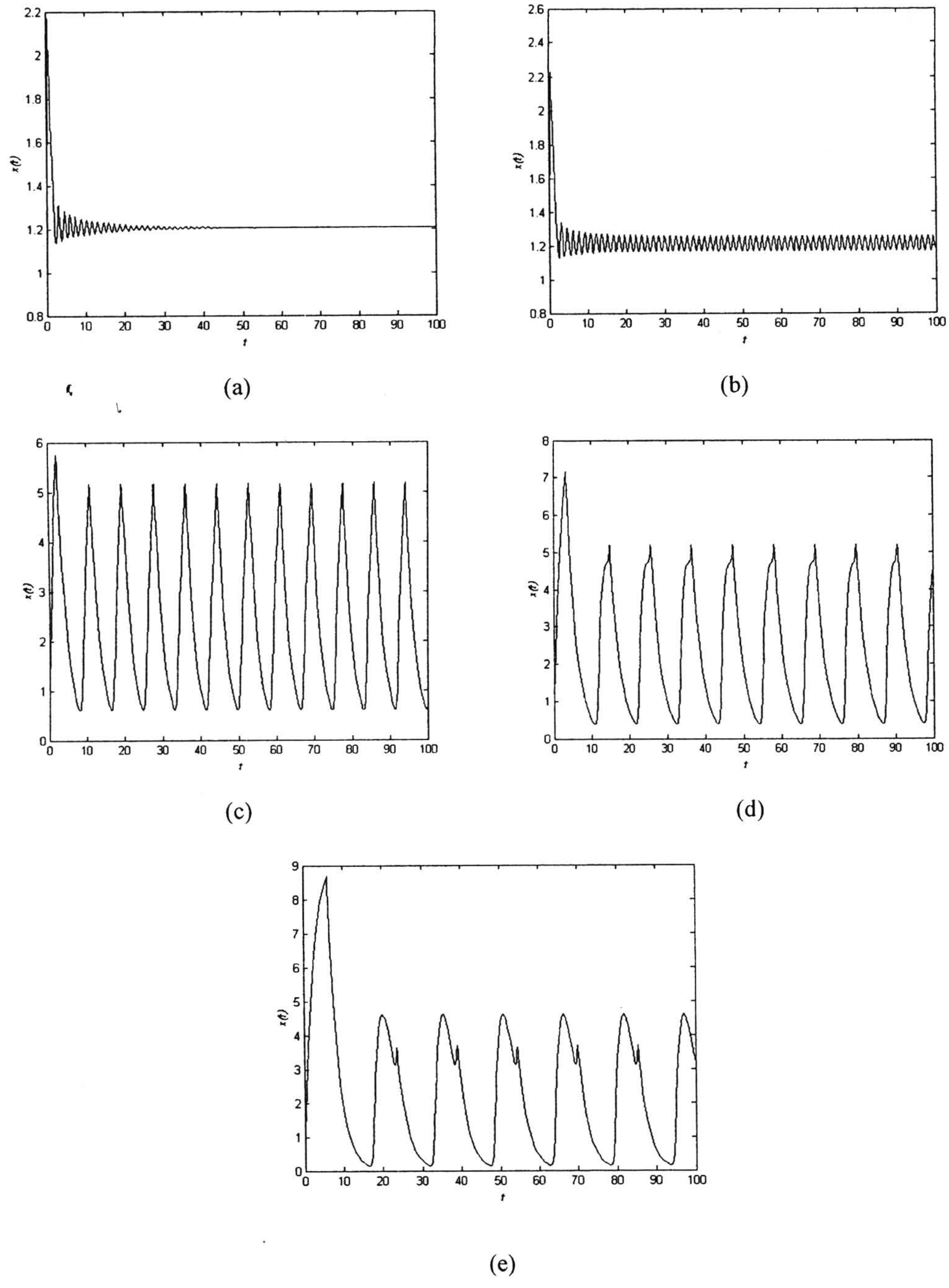

FIGURE 3-1 Numerical solutions of (3-20) with different values of τ, where (a) $\tau = 0.37$, (b) $\tau = 0.39$, (c) $\tau = 2.1$, (d) $\tau = 3.3$ and (e) $\tau = 6.0$.

3.4.2 The Nicholson's blowflies equation

We consider the equation which proposed by Gurney *et al.* [13]

$$N'(t) = -\gamma N(t) + \beta N(t-\tau)e^{-aN(t-\tau)}; \qquad t \geq 0, \tag{3-32}$$

where $N(t)$ represents the density of population, β is the maximum *per capita* daily egg production rate, $1/a$ is the size at which the blowfly population reproduces at its maximum rate, γ is the *per capita* daily adult death rate and τ is a positive constants [23].

Comparing equations (3-18) and (3-32), we can see that

$$f(N) = e^{-aN}, \tag{3-33}$$

and

$$f^{-1}(N) = -\frac{1}{a}\ln N. \tag{3-34}$$

The equilibrium $\tilde{N}$ of (3-32) can be determined. If $\beta > \gamma$, then there exists the unique positive equilibrium:

$$\tilde{N}_+ = f^{-1}\left(\frac{\gamma}{\beta}\right) = -\frac{1}{a}\ln\left(\frac{\gamma}{\beta}\right). \tag{3-35}$$

It is not difficult to show that $f(\tilde{N}_+)$ and $f'(\tilde{N}_+)$ in the form

$$f(\tilde{N}_+) = \frac{\gamma}{\beta}, \tag{3-36}$$

and

$$f'(\tilde{N}_+) = -a\frac{\gamma}{\beta}. \tag{3-37}$$

Replacing $\tilde{N}_+, f(\tilde{N}_+)$ and $f'(\tilde{N}_+)$ from (3-35)-(3-37) to

$$\eta = \beta\big(f(\tilde{N}_+) + \tilde{N}_+ f'(\tilde{N}_+)\big),$$

then the Hopf bifurcation points $\tau_0, \tau_1, \tau_2, \ldots, \tau_k$, where $k = 0, 1, 2, \ldots$ can be calculated from the following equations:

$$\tau_k = \frac{1}{\sqrt{\eta^2 - \gamma^2}}\left[\arccos\left(\frac{\gamma}{\eta}\right) + 2k\pi\right]; \qquad \eta < 0, \tag{3-38}$$

or

$$\tau_k = \frac{1}{\sqrt{\eta^2 - \gamma^2}}\left[2\pi - \arccos\left(\frac{\gamma}{\eta}\right) + 2k\pi\right]; \quad \eta > 0, \tag{3-39}$$

with the condition

$$\eta = \gamma\left(1 + \ln\left(\frac{\gamma}{\beta}\right)\right). \tag{3-40}$$

As the results, the Nicholson's blowflies with the delay τ as the bifurcation parameter undergoes a Hopf bifurcation when $\tau > \tau_0$.

To support the results in the previous section, we present some numerical results generated by Matlab®. The parameter values of (3-32) are placed as $n = 13$, $\beta = 5.0$, $\gamma = 0.4$, $a = 0.1$, and the initial function $x(t) = 0.8$, where $t \in [-\tau, 0]$. Then, we also find η from (3-40) by replacing β and γ

$$\eta = -0.6103. \tag{3-41}$$

The Hopf bifurcation point τ_0, τ_1 and τ_2 are evaluated by replacing the values of η and γ from (3-41) into (3-38). It follows that

$$\tau_0 = 4.9584,\ \tau_1 = 18.5896 \text{ and } \tau_2 = 32.2209. \tag{3-42}$$

Finally, we show some numerical simulations of the model (3-32) with different values of delays. Firstly, If $\tau = 4.4 < \tau_0 \approx 4.9584$, as defined in (3-42), then $\tilde{N}_+$ is asymptotically stable (see Figure 3-2(a)). On the contrary, the numerical solutions showing in Figure 3-2 (b)-(e), we use different values of delays, namely $\tau = 5.0 > \tau_0$; $\tau = 20.0 > \tau_1$; $\tau = 33.0 > \tau_2$ and $\tau = 64.0 \gg \tau_2$, respectively. All solutions are oscillated about the equilibrium $\tilde{N}_+$, i.e. it is unstable. Thus, from the numerical simulation, it follows the analytical result that the positive equilibrium $\tilde{N}_+$ is asymptotically stable when $\tau \in (0, \tau_0)$, and it undergoes a Hopf bifurcation (unstable) when $\tau > \tau_0$.

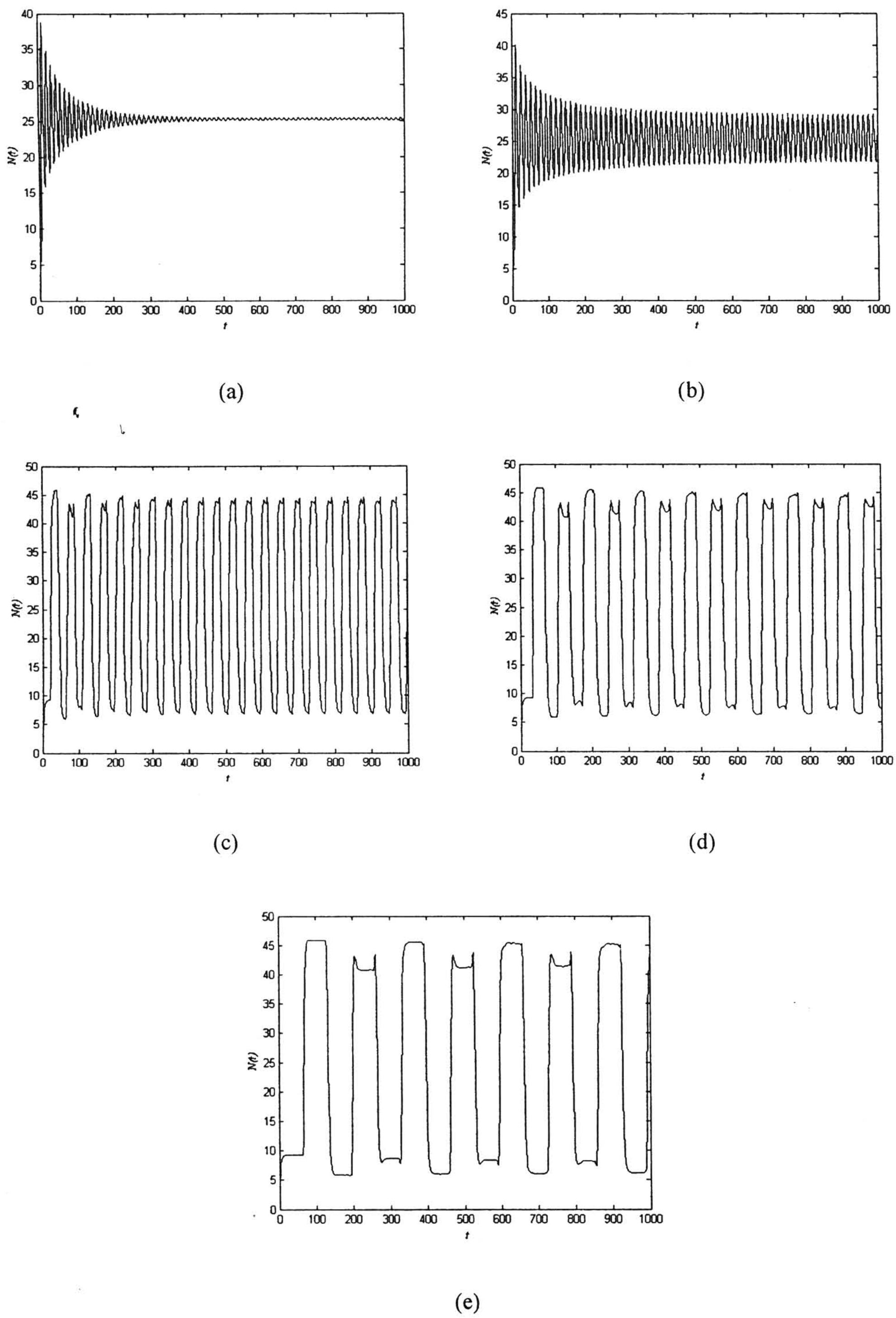

FIGURE 3-2 Numerical solutions of (3-32) with different values of τ, where (a) $\tau = 4.4$, (b) $\tau = 5.0$, (c) $\tau = 20.0$, (d) $\tau = 33.0$ and (e) $\tau = 64.0$.